CONTRASTING LIFESTYLES IN LOWER JURASSIC CRINOIDS: A COMPARISON OF BENTHIC AND PSEUDOPELAGIC ISOCRINIDA

by MICHAEL J. SIMMS

ABSTRACT. Lower Jurassic pentacrinitids have been regarded either as pseudopelagic in habit, living suspended beneath floating objects such as driftwood, or as strictly benthic, living much like all known representatives of their sister group the Isocrinidae. The taphonomy of Lower Jurassic pentacrinitids differs significantly from that of contemporary isocrinids in their environments of preservation, extent of disarticulation, occurrence in debris accumulations, frequency of association with driftwood, and the size and position of the driftwood relative to the crinoids. Unlike contemporary Isocrinidae, Lower Jurassic pentacrinitids have a low overall population density, wide geographical distribution, and rapid growth to reproductive maturity, indicated by the growth lines on brachials and by the high filtration efficiency of the endotomous arm branching. A high fecundity is implied by the large size of adult pentacrinitids and the high concentration of larval attachment discs on driftwood. These taphonomic, palaeobiological and morphological features of pentacrinitids are consistent with those which might be anticipated for pseudopelagic organisms suspended beneath temporarily floating objects of limited availability and subject to wide dispersal. The evolutionary stasis shown by the pentacrinitid *Seirocrinus subangularis* (Miller), which persisted from the Carixian into the mid-Toarcian, is remarkable considering the profound faunal changes which occurred in the early Toarcian and suggests that this species was not influenced by changes in the benthic environment.

Although Lower Jurassic pentacrinitids are here considered essentially as obligate pseudoplankton, there is some evidence that occasional specimens may have survived as benthic crinoids after sinking into a favourable environment.

MORE than twenty species of crinoid are known from the British Lower Jurassic, most of which can be assigned to two closely related families, the Isocrinidae Gislén and the Pentacrinitidae Gray. These two families differ significantly not only in their morphology but also in the way in which they are commonly preserved, suggesting some fundamental difference in their respective modes of life.

The Isocrinidae includes many living species and recent observations of isocrinids in their natural environment has added greatly to our understanding of how they live (Conan *et al.* 1981; Macurda and Meyer 1974, 1983; Rasmussen 1977). All living and fossil Isocrinidae are believed to be strictly benthic, rheophilic crinoids attaching to sea-floor debris or directly to the substratum by means of the cirri which arise from the stem at regular intervals.

The Pentacrinitidae have no living representatives and are most commonly preserved as intact groups associated with coalified driftwood in organic-rich shales and mudstones.

William Buckland (1836), 150 years ago, noted the occurrence of *Pentacrinites fossilis* Blumenbach beneath lenses of coalified driftwood in the Sinemurian of the Dorset coast and proposed that they had lived suspended beneath floating driftwood. More recently Seilacher *et al.* (1968) and Haude (1980) have supported this view and put forward further evidence suggesting that pentacrinitids had a pseudopelagic mode of life. This hypothesis has been challenged by others (Abel 1927; Rasmussen 1977; Kauffman 1981) who interpret pentacrinitids as being strictly benthic, like the contemporary isocrinids.

This paper sets out to examine the evidence for and against a pseudopelagic mode of life in Lower Jurassic pentacrinitids.

APPROACH AND METHODOLOGY

In trying to reconstruct the mode of life of fossil crinoids there are three principal lines of evidence that can be used: taphonomy, functional morphology, and palaeobiology. Although the style of preservation generally reflects the way in which an animal met its death, it can also give insight into how the animal was living prior to this event. A series of taphonomic paradigms have been constructed for both benthic and pseudopelagic crinoids against which the taphonomic history of fossil isocrinids and pentacrinitids can be compared. This represents a modification of Rudwick's (1964) paradigm approach in which one or more functions are postulated for a given structure, each function then being used to define an abstract mechanical model called a paradigm. The paradigm which most closely approximates to the actual structure will then indicate the most probable function for that structure. In the case of the taphonomic paradigm, certain taphonomic features should differ considerably between benthic and pseudopelagic crinoids. It should, therefore, prove possible to determine whether pentacrinitids were benthic or pseudopelagic on the basis of the paradigm to which their actual taphonomic history most closely approximates. In addition, certain palaeobiological factors are considered in relation to a pseudopelagic lifestyle in crinoids. The functional significance of those morphological features unique to pentacrinitids are also assessed in the light of the two contrasting habits.

Much previous work on the mode of life of Lower Jurassic pentacrinitids has tended to concentrate on the highly specialized *Seirocrinus subangularis* (Miller) from the Toarcian Posidonienschiefer (Seilacher *et al.* 1968; Kauffman 1981). In the present work I have concentrated largely on the less advanced *P. fossilis* Blumenbach from the Sinemurian of the Dorset coast. Numerous specimens from this site can be found in virtually every museum with a geological collection, but are seldom associated with accurate location data. Lang and Spath (1926) described the Black Ven Marls (Sinemurian) of the Dorset coast in considerable detail but perpetuated the idea of previous authors that the specimens of *P. fossilis* were restricted to a single impersistent horizon, the 'Pentacrinite Bed', about 4 ft above the Upper Flatstones on Black Ven, west of Charmouth. *P. fossilis* has not been seen *in situ* on Black Ven during the course of this study but has been observed *in situ* on several occasions on Stonebarrow, to the east of Charmouth. This has revealed that *P. fossilis* occurs most abundantly between 2 and 4 m above the Stonebarrow Flatstones but is not restricted to particular horizons within this 2 m interval. Observations by local collectors suggest that specimens may occur sporadically somewhat lower in the succession; a short distance below the Stonebarrow Flatstones (S. Barnsley, pers. comm.) and just above the Birchi Tabular (Lang Coll., BMNH E26451–26458, E51525–51526, E51528). The occurrence of *P. fossilis* at more than one horizon on Stonebarrow has also been reported by Jackson (1966).

The following abbreviations are used: BMNH, British Museum (Natural History); OUM, Oxford University Museum; WARMS, Warwick Museum.

EVIDENCE FROM TAPHONOMY

Five taphonomic paradigms have been constructed in which one might expect benthic and pseudopelagic crinoids to differ. These are listed in Table 1 and are discussed individually below.

Paradigm 1, Facies distribution

Whereas benthic crinoids might be expected to occur in a restricted range of environments usually associated with other benthic organisms, pseudopelagic crinoids should be facies independent.

Representatives of the Isocrinidae are frequent elements of normal benthic faunas in facies ranging from mudstones through silts and sands to coarse oolites. Individual species, however, occupy a much more restricted facies range. In Britain, *Balanocrinus quiaiosensis* Loriol only occurs in association with abundant shell debris on muddy substrata, whereas *Chladocrinus scalaris* (Goldfuss) is rare in such an environment and grows to only half the size of those in a siltier facies, where it is much more abundant. Isocrinids are virtually unknown in finely laminated shale facies. I have encountered only two such specimens from the British Lower Jurassic (WARMS G9921 and OUM J3231). Both are

TABLE 1. Taphonomic paradigms for benthic and pseudopelagic crinoids.

Benthic crinoids.	Pseudopelagic crinoids.
1. Facies dependent.	Facies independent.
2. Fully articulated preservation rare and due to death by sudden burial.	Fully articulated preservation common due to sinking into anoxic environments.
3. Moderate to high population densities contribute significantly to benthic shell beds.	Low overall population densities do not contribute to shell beds.
4. Sometimes associated with driftwood; attached to side or upper surface.	Very often associated with driftwood; attached to side or lower surface.
5. Crinoid size unrelated to driftwood size.	Crinoid size proportional to driftwood size.

exceptionally well-preserved specimens of *C. psilonoti* (Quenstedt) from an unrecorded horizon in the Hettangian or Lower Sinemurian of Dorset.

In contrast most specimens of *Pentacrinites* and *Seirocrinus* from the Lower Jurassic have been obtained from organic-rich shales or mudstones. In Dorset, *P. fossilis* is primarily confined to the lower part of the Black Ven Marls, in the *obtusum* Subzone (bed 84 of Lang and Spath 1926), where specimens occur in dark, organic-rich shales and mudstones. This part of the succession is rich in ammonites but, except for one or two very thin horizons containing small specimens of *Plagiostoma*, it lacks any significant benthic fauna. This suggests that the environment was anoxic. Very small (up to 1 mm) specimens of *Protocardia*, *Liostrea*, and *Grammatodon* are often abundant throughout bed 84 and are interpreted as bivalve spat which settled in an unfavourable environment and quickly died. Large adult individuals of *Oxytoma*, *Gervillia*, and *Cuneigervillia* are also encountered in these deposits but all are byssate forms which may have fallen from floating objects. Attachment of byssate bivalves to floating driftwood is well documented (Seilacher 1982) and many specimens demonstrating this are known from the *obtusum* Subzone of Dorset (e.g. BMNH LL18767). Thus if *Pentacrinites fossilis* is interpreted as a benthic crinoid, as proposed by Rasmussen (1977), then it represents the only normally developed benthic organism in an otherwise barren environment. Similarly *P. dichotomus* (M'Coy) from the Toarcian, *S. subangularis* (Miller) from the Pliensbachian to Toarcian, and an undescribed species of *Pentacrinites* from the Hettangian to Lower Sinemurian are all found most frequently in organic-rich deposits such as the Bituminous Shales of Yorkshire and the Posidonienschiefer of Southern Germany.

However, occasional specimens have been found in facies containing a reasonably well-developed benthic fauna. A large group of well-preserved individuals of *Pentacrinites* sp. nov. from the *bucklandi* Zone of Keynsham, Avon (BMNH E25102) is preserved in a muddy limestone containing ammonites (*Arietites* sp. and ?*Epammonites*) and rhynchonellid brachiopods. Material from a similar facies is also known from Gloucestershire (BMNH E122). The significance of these specimens is discussed under paradigm 2.

The high proportion of specimens recorded from organic-rich facies and the great rarity of those from higher energy environments does not, however, suggest that Lower Jurassic pentacrinitids had an ecological preference for such hostile environments. This apparently unequal distribution is more likely to reflect the much greater potential for preservation of articulated specimens in anoxic environments. In addition, the low population density characteristic of pentacrinitids, discussed under paradigm 3, renders disarticulated ossicles, such as would be found in non-anoxic facies, considerably rarer than ossicles from benthic species. Finally, a very considerable collecting bias inevitably operates here since isolated ossicles are far less likely to be noticed, or collected, than intact specimens.

The wide range of environments in which pentacrinitids occur suggests they were not confined to specific benthic habitats and is compatible with their having lived pseudopelagically.

## Paradigm 2, Extent of disarticulation

Preservation of fully articulated benthic crinoids is rare and generally due to death by sudden burial. Pseudopelagic crinoids can also be preserved intact but primarily in anoxic environments into which they sank.

The benthic Isocrinidae are prone to disarticulate rapidly through bacterial decay of soft tissues, current action, and the activities of scavengers and other vagile benthos in normal marine environments (Meyer 1971a; Liddell 1975). Fully articulated specimens are comparatively rare and are usually the result of death through burial by a rapid influx of sediment to a depth sufficient to prevent subsequent bioturbation. Rosenkranz (1971) has described such an occurrence in the Hettangian of southern Germany and there are numerous other examples in the British Lower Jurassic. In such cases both the upper and lower surfaces of specimens are equally well preserved. Sediment generally envelops the individuals and frequently lies between the arms on the lower and the upper surface and between different individuals (Pl. 36, fig. 2).

Unlike isocrinids the Pentacrinitidae are usually found intact. As discussed in paradigm 1 this can occur when the crinoid sinks into an anoxic environment. In such cases burial generally occurs some time after death of the crinoids and is a gradual process, so that the upper surface of the specimens is exposed to the action of currents and occasional vagile organisms which may subsequently move across the surface. Such a style of preservation is very common in specimens of *P. fossilis* from the Dorset coast and has also been reported for specimens of *S. subangularis* from the Posidonienschiefer (Kauffman 1981). Many specimens from Dorset show little or no disruption of the lower surface (text-fig. 1a) but invariably show some degree of disarticulation of the upper surface, often with winnowing and size-sorting of the ossicles clearly representing the action of currents for some time after the death of the crinoids (text-fig. 1b). Other specimens also show significant disruption of the lower surface in the form of resting and crawling traces of vagile benthic organisms, possibly crustacea, which penetrate through to the lower surface as sharply defined patches of disarticulated ossicles (Pl. 36, figs. 1 and 3). Such disruption without total disarticulation may be due to specimens sinking into a poorly oxygenated environment with a very sparse benthic fauna. Alternatively, a brief return to oxygenated conditions may occur before the crinoids have been buried to a sufficient depth to prevent subsequent bioturbation. This may be the case in one specimen (BMNH E69600) in which

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EXPLANATION OF PLATE 36

Fig. 1. Disruption of arms and pinnules by crawling traces on lower surface of '*Pentacrinites* Bed', Sinemurian, *obtusum* Subzone, Black Ven, Charmouth, Dorset. BMNH E69605, × 1.

Fig. 2. Intact preservation of *Balanocrinus gracilis* (Charlesworth) with specimens enveloped by sediment. Domerian, *stokesi* Subzone, Robin's Wood Hill, Gloucester. BMNH E69629, × 0·8.

Fig. 3. Vertical section through lenticle of '*Pentacrinites* Bed' and surrounding limestone. The crinoid remains are cemented by diagenetic calcite overgrowths, with virtually no interstitial sediment. Disruption caused by an unknown organism is visible towards the right of the specimen. Sinemurian, *obtusum* Subzone, Black Ven, Charmouth, Dorset. BMNH E69607, × 1·1.

Fig. 4. Endotomous branching of arms in *Pentacrinites fossilis* Blumenbach. Lower Lias, Lyme Regis, Dorset. BMNH E50579, × 0·5.

Fig. 5. Isotomous branching of arms in the isocrinid *Chladocrinus robustus* (Wright). Carixian, *daveoi* Zone, Mickleton Tunnel, Gloucestershire. BMNH E1498, × 0·65.

Fig. 6. Short-stemmed specimen of *P. fossilis* Blumenbach attached to lower surface of coalified driftwood by recurved cirri. The line marks the edge of the driftwood which is here obscured by a layer of 'beef', visible in the upper part of the figure. Sinemurian, *obtusum* Subzone, bed 84, Stonebarrow, Charmouth, Dorset. BMNH E69600, × 0·6.

Fig. 7. Variation along the stem of *P. fossilis* Blumenbach. Cirriferous proximal stems are visible in the upper part of the figure. In the lower part is a bundle of stems from a more distal region with short, widely spaced cirri. Sinemurian, *obtusum* Subzone, Stonebarrow, Charmouth, Dorset. BMNH E69603, × 1.

Fig. 8. Symplexial articulation on aboral face of cirrinodal of *P. fossilis* Blumenbach. Sinemurian, *obtusum* Subzone, bed 84, Stonebarrow foreshore, Charmouth, Dorset. BMNH E69606, × 3·6.

PLATE 36

SIMMS, Lower Jurassic crinoids
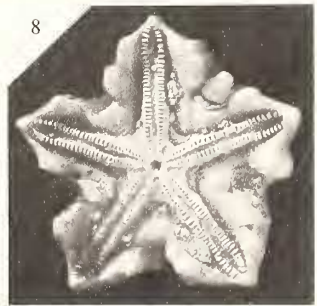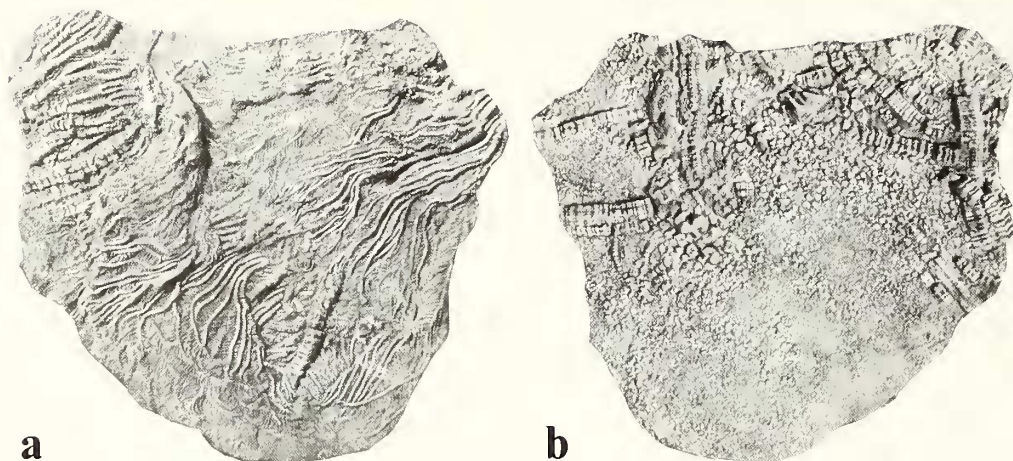
TEXT-FIG. 1*a*, intact preservation of *Pentacrinites fossilis* Blumenbach on lower surface of '*Pentacrinites* Bed'. Sinemurian, *obtusum* Subzone, Black Ven, Charmouth, Dorset. BMNH E69604, ×0·5, *b*, disarticulation and winnowing of stems and brachials on upper surface of same specimen.

a thin shelly layer with *Plagiostoma* and *Liostrea* is separated from a bioturbated group of crinoids beneath by a few millimetres of dark, organic-rich shale.

An alternative possibility for these disrupted areas is that they represent the effects of degassing during decomposition. Disarticulation on the upper surface of all specimens from Dorset shows that decomposition of soft tissues occurred to some extent even in the most anoxic environment, yet the features under discussion are seen only in certain specimens. This explanation thus seems unlikely.

Further evidence that the intact preservation in pentacrinitids is due to the anoxicity of the environment, rather than death by burial, is seen from the general absence of any interstitial sediment within groups of these crinoids. Specimens of *Pentacrinites fossilis* from the Dorset coast and elsewhere are characteristically preserved as thin limestone lenticles produced by the diagenetic overgrowth of the calcite of the skeleton into the interstices between the ossicles (Pl. 36, fig. 3). Sediment inclusions, where present, are always very minor suggesting a slow rate of sediment accumulation.

Although Lower Jurassic pentacrinitids are usually preserved intact in anoxic environments, one group of individuals of *Pentacrinites* sp. nov., from the *bucklandi* Zone of Keynsham, Avon (BMNH E25102), appears to have been killed and preserved by a rapid influx of coarse sediment. The specimen was collected in the early nineteenth century (Parkinson 1808; Townsend 1813) and no field observations are available. However, the upper surface shows negligible disarticulation and a significant interstitial sediment component is present, thus resembling the style of preservation characteristic of benthic isocrinids. This specimen is of considerable importance since it suggests that pentacrinitids were quite capable of surviving as benthic crinoids if they sank into a reasonably favourable environment.

Paradigm 3, Debris accumulations

Benthic crinoids frequently attain moderate to high population densities and may contribute significantly to benthic shell beds. Pseudopelagic crinoids should have a low overall population density and so cannot contribute significantly to benthic shell beds.

Crinoidal limestones and other accumulations of crinoid debris are common features of many Lower Jurassic sequences but are composed only of isocrinid debris. Pentacrinitids are only represented as rare isolated ossicles in such accumulations and this suggests they existed in much

lower population densities than contemporaneous benthic crinoids. One possible factor causing this may be the limited availability of suitable floating objects for attachment, such as driftwood. Another possible cause has been documented by Schäfer (1972, p. 122) for the pseudopelagic cirripede, *Lepas*. Such a mode of life encourages a wide geographical distribution but diminishes the density of populations. After death the skeletal parts of *Lepas* fall individually to the sea-floor as the soft tissues decay and are thus spread over a wide area and never contribute significantly to shell beds on the sea-floor. A very similar situation seems to prevail in pentacrinitids, with isolated ossicles being rare and widely scattered.

*Paradigm 4, Association with driftwood*

Association of benthic crinoids with sunken driftwood is occasional and fortuitous, with the crinoids attaching to the upper surface of the driftwood. Pseudopelagic crinoids are often associated with driftwood and invariably attach to the lower surface of the driftwood.

Most Lower Jurassic isocrinids must have adopted a posture like that portrayed by Rasmussen (1977, fig. 2) with the stem anchored directly to the substratum by the cirri, much as in extant isocrinids (Conan *et al.* 1981; Macurda and Mayer 1974, 1983). Available sea-floor debris, including driftwood could also have been utilized for anchorage. Inevitably in such cases the crinoids could only have attached to the side or top of the driftwood and are not found beneath it (BMNH E69601).

Lower Jurassic pentacrinitids are found associated with coalified driftwood with much greater frequency. In all well-documented examples of *P. fossilis* from the Dorset coast found in association with driftwood, the crinoids have been found to lie at least partly beneath the driftwood, as noted by several previous collectors (Buckland 1836; Jackson 1966). The consistent occurrence of coalified driftwood overlying the crinoids is very difficult to explain plausibly without invoking a pseudo-pelagic mode of life. Pseudopelagic crinoids will have lived suspended beneath a floating log and will therefore have been trapped beneath it when the log eventually sank to the sea-floor (text-fig. 2a, b). Haude (1980) considered that increasing hydrostatic pressure as the log sank would have decreased its buoyancy and thus accelerated its rate of descent so that it would have come to settle on the bottom before the crinoids. This seems a very plausible hypothesis but the evidence from specimens on the Dorset coast does not support it.

Isolated individuals or small groups of pentacrinitids are not always found associated with driftwood. It is probable that such specimens became accidentally detached from the driftwood whilst it was still afloat and sank to the bottom where they were preserved due to anoxic conditions.

Further strong evidence for attachment of pentacrinitids to floating driftwood is provided by the distribution of larval attachment discs of crinoids on a piece of coalified driftwood (text-fig. 2c) recently discovered on the Dorset coast. In this specimen, as in many others from the Black Ven Marls, the driftwood has been compressed without any significant lateral distortion (Briggs and Williams 1981) so that the lower surface represents the lower half of the floating log and the upper surface the upper half. The lower surface of this particular specimen is obscured by undisturbed adult specimens of *P. fossilis* but the marginal 2 cm of the upper surface is covered with numerous very small attachment discs of larval crinoids, almost certainly belonging to *P. fossilis*. The remainder of the upper surface is devoid of any larval discs except for a small group about 7 cm from the driftwood margin. The specimen as preserved has a maximum width of 12 cm but clearly represents part of a much larger log more than 20 cm in diameter. The straight edge of the specimen represents the side of the floating log and the absence of a significant number of attachment discs towards the centre, representing the upper part of the log, strongly suggests that it was colonized whilst floating at the surface with the uppermost part projecting above the water. Initial colonization would be on the lower surface but as this became crowded with the rapidly growing crinoids and the driftwood sank lower in the water further settlement of larval crinoids would be restricted to higher, less favourable areas exposed to greater turbulence. However, a large area of the upper surface would remain uncolonized as long as the driftwood was afloat because of its exposed position at or close to the water surface. Upon sinking to the sea-floor this area would become accessible to settling crinoid larvae. However, it is evident that no further settlement took place once the driftwood had reached

a
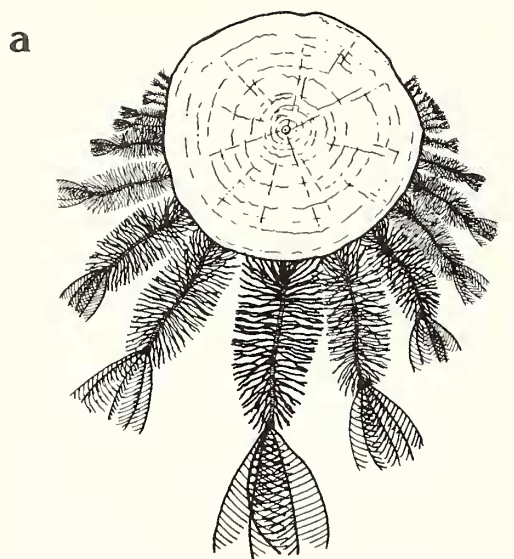
TEXT-FIG. 2. Distribution of crinoids on floating drift-wood. *a*, diagrammatic reconstruction of crinoid distribution on floating driftwood reflecting colonization by successive generations of larvae on progressively higher parts of the driftwood. *b*, cross-sectional appearance of crinoids and driftwood after burial and compression. The larger crinoids are seen as a white layer extending from beneath the coalified driftwood whilst the last generation of larvae to settle prior to sinking of the driftwood are found along the margins of the upper surface of the compressed driftwood. *c*, distribution of larval attachment discs (dots) of *Pentacrinites fossilis* Blumenbach on the upper surface of a fragment of compressed and coalified driftwood. The hatched area in the lower part of the figure represents the larger crinoids extending from beneath the driftwood. Sinemurian, *obtusum* Subzone, Black Ven, Charmouth, Dorset. BMNH E69602.

b

c

5 cm
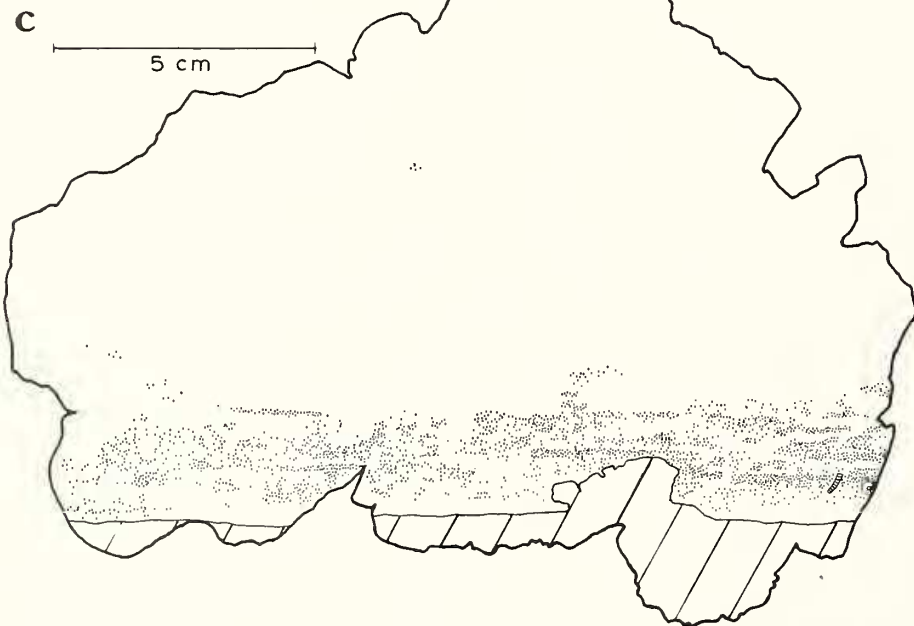
TEXT-FIG. 3. Plot of maximum columnal diameter/driftwood diameter for Isocrinidae and Pentacrinitidae associated with driftwood. Pentacrinitid size is correlated with driftwood size, whereas that of Isocrinids is not. Columnal diameter is used as a size index because of the fragmentary nature of most isocrinid material. Based on museum material and observation of specimens *in situ.*
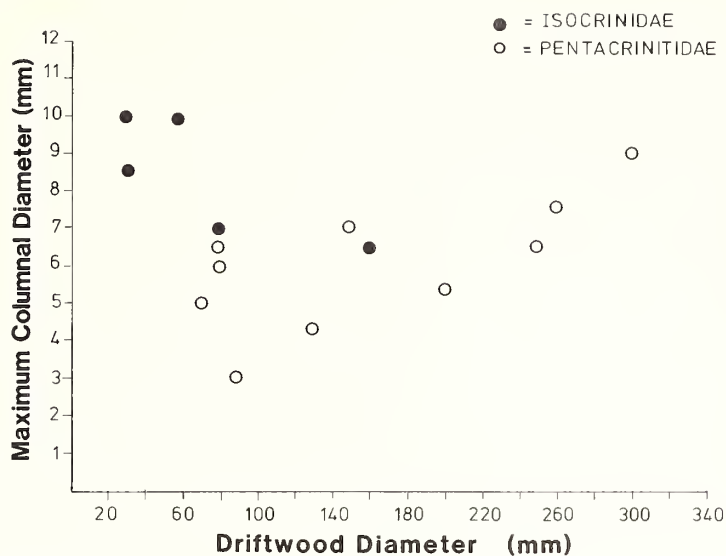
the sea-floor and that those larvae already present perished along with the mature individuals on the lower surface. Since larval pentacrinitids were clearly unable to become established in the environment in which we now find them, none could have survived to maturity and so those specimens found must represent allochthonous faunal elements.

Paradigm 5, Crinoid/Driftwood size correlation

Since the weight of pseudopelagic crinoids has to be supported by the floating driftwood one would expect there to be a correlation between the size of the crinoids and of the driftwood. No such correlation would be expected where benthic crinoids are found in association with sunken driftwood since the driftwood serves merely as a temporary anchor.

In the case of isocrinids associated with driftwood no correlation has been observed between the size of the crinoids and that of the driftwood. Specimens of *Chladocrinus psilonoti* with a stem diameter of almost 10 mm have been found attached to pieces of driftwood less than 30 mm in diameter. However, specimens of *Pentacrinites* and *Seirocrinus* from Britain and Germany do show some correlation between crinoid size and driftwood size (text-fig. 3) although data are somewhat limited due to inadequate collection of specimens in the past. Coalified driftwood of all sizes up to several metres in length is abundant in the *obtusum* Subzone on the Dorset coast but crinoids are only rarely found attached to the smaller pieces. The largest specimens are always found attached to correspondingly large masses of driftwood. One such specimen from Dorset (BMNH E69840) comprises a mass of driftwood 26 cm in diameter and almost 2 m long to which are attached several hundred large *P. fossilis* with arms more than 140 mm long in some cases. Smaller masses of driftwood have fewer and smaller specimens of *P. fossilis* attached (BMNH E69600).

The load capacity of a floating log was calculated by Haude (1980) for a specimen from the Toarcian Posidonienschiefer and he found that the attached load of bivalves and crinoids was just sufficient to cause the driftwood to sink.

EVIDENCE FROM FUNCTIONAL MORPHOLOGY AND PALAEOBIOLOGY

Comparison of the taphonomy of Lower Jurassic isocrinids and pentacrinitids favours a pseudopelagic mode of life for the latter group. Any pseudopelagic crinoid should be expected to differ

significantly from benthic crinoids in a number of features because of the morphological and palaeobiological constraints imposed by these two fundamentally different lifestyles. Major controlling factors for a pseudopelagic mode of life include the characteristically low population density of such organisms, the limited floating duration of the attachment site, and the pendent lifestyle. Considering these factors in relation to the morphology of Lower Jurassic pentacrinitids should, therefore, provide further evidence about their mode of life.

Population density

Pseudopelagic organisms characteristically have a low overall population density due to the limited availability of suitable floating attachment sites and the wide dispersal of these by ocean currents. However, such organisms are invariably densely gregarious on suitable floats because of the rarity of floating logs. The chances of successful cross-fertilization are thus enhanced.

Most Lower Jurassic pentacrinitids are found as tangled groups of many individuals of various sizes associated with coalified driftwood. Kauffman (1981) mentions many isolated specimens of *Seirocrinus* and *Pentacrinites* found in the Posidonienschiefer unassociated with driftwood. He interprets these as benthic crinoids attached directly to the substratum but an equally plausible explanation is that they represent individuals which inadvertently became detached from their floating anchorage.

In contrast, benthic isocrinids might be expected to be densely populated over large areas but without particular local concentrations. For example *Balanocrinus gracilis* (Charlesworth) is found in considerable abundance evenly distributed across extensive bedding planes in the *stokesi* Subzone at Staithes, on the Yorkshire coast.

Growth and maturation

A major obstacle to the pseudopelagic model for Lower Jurassic pentacrinitids is the apparent discrepancy between the supposed floating life of a piece of driftwood and the considerably greater length of time believed necessary for crinoids to attain the large size seen in certain specimens. Kauffman (1975, 1981) stated that most wood sinks in less than a year because it becomes waterlogged, whilst Haude (1980) quoted 1·5-2 years as the maximum duration for which an unloaded conifer trunk would float in rivers of the Northern hemisphere. However, recent observations suggest estimates such as these are unduly short since more than 50% of the conifer trunks which jammed Spirit Lake following the eruption of Mount St Helens in May 1980 were still afloat five years later (R. A. Spicer, pers. comm.). It is possible that bacterial sealing of vessels may enable driftwood to float for perhaps even ten years or more whilst the density of seawater and also the osmotic pressure which it exerts on the moisture content of the wood will further enhance the buoyancy and floating duration of driftwood in marine environments.

Figures such as these greatly extend the time available for maturation of the crinoids. However, the actual floating duration of a particular mass of driftwood is determined by many factors and is hence unpredictable. Furthermore, the initial colonization by crinoid larvae may not occur until the driftwood has been afloat for some time. Therefore, in order to ensure that they reproduce before the driftwood sinks, the crinoids must reach maturity as rapidly as possible. This is most readily achieved by paedomorphosis, where reproductive maturity is reached in juvenile forms. However, penta-crinitids frequently attain a very large size, with an arm length of as much as 40 cm in some examples of *S. subangularis*, and were clearly not paedomorphic. Only a rapid growth rate can account for this large size. No data are available concerning the growth rate of extant isocrinids but brachials of *C. tuberculatus* (Miller), from the Sinemurian of Gloucestershire, show growth lines indicating four or five years are required to attain an arm length of about 10 cm. Comparable sized brachials of *P. fossilis* from Dorset, however, show only two or three growth lines (text-fig. 4). Growth-line spacing in both of these species also indicates that growth was most rapid in the first year, decreasing thereafter. A similar pattern of growth has also been reported by Whyte (1982) for the Carboniferous inadunate *Parazeacrinites konincki* (Bather).
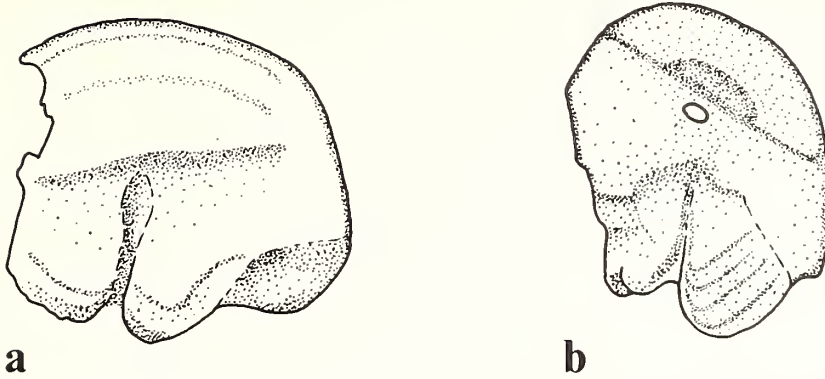
TEXT-FIG. 4. Growth lines on brachials, × 10. *a*, secundibrach of *Pentacrinites fossilis* Blumenbach in third year of growth (BMNH E69608). *b*, secundibrach of *Chladocrinus tuberculatus* (Miller) in fifth year of growth (BMNH E69628).

The different pattern of arm branching in isocrinids and pentacrinitids also indirectly suggests a more rapid growth rate is characteristic of the latter. In most isocrinids the pattern of arm branching is isotomous throughout with the arms bifurcating at intervals up to five or six divisions (Pl. 36, fig. 5). In *Pentacrinites* and *Seirocrinus* the pattern of arm branching is essentially endotomous (Pl. 36, fig. 4) with up to twenty-six divisions per arm. The first two arm divisions are isotomous but thereafter all succeeding divisions are endotomous, arising from outer branches in relation to secundibrachs with the long inner branches remaining undivided except for *S. subangularis* in which the first inner branch shows further endotomous branching in its distal region. Such a pattern of arm branching is reminiscent of that seen in certain camerate Melocrinitidae (Brower 1976). Cowen (1981) developed Brower's observations further and drew an analogy between the pattern of arm branching in advanced melocrinitids and the ideal layout for harvesting roads on a banana plantation. The arms of melocrinitids and pentacrinitids are seen to represent the optimum arrangement for an efficient filtration network with the minimum expenditure of energy and materials in construction. The resultant filtration fan is significantly more efficient, with fewer gaps between pinnules, than is found in most isocrinids. Attainment of almost complete pinnulation is achieved by the loss of syzygies in the arms, a feature peculiar to Lower Jurassic pentacrinitids and not seen in other Isocrinida. Pinnules are lacking on hypozygal brachials in other Isocrinida and so the loss of this type of articulation in pentacrinitids may be related more to the evolution of an efficient filtration fan than to the function of syzygies as autotomy points in the arms. This improved food gathering efficiency would contribute significantly to a rapid growth rate and attainment of large size. However, despite the apparent efficiency of this pattern of arm branching, Cowen remarked on how infrequently such an arrangement has evolved in crinoids. In this respect it is perhaps significant to note that the Late Devonian *Melocrinites*, which most closely approaches the ideal model, is found in dark shales in association with coalified driftwood and has also been suggested as being pseudopelagic (Wells 1941; McIntosh 1978).

Geographical distribution

Pseudopelagic crinoids are subject to dispersal by ocean currents and so might be expected to have a wider geographical distribution than benthic crinoids. Unfortunately, very few reliable data are available concerning the geographical distribution of Lower Jurassic crinoids. Although no species of isocrinid found in Britain, such as *C. tuberculatus* (Miller), has yet been found outside of Eurasia (Biese 1936; Klikushin 1982) the pentacrinitid *S. subangularis* has a wider range than any other Liassic crinoid. Specimens have been recorded from Britain and Europe, northern Alaska (Springer 1925),

eastern Siberia (Klikushin 1982), and the Soviet Far East (Klikushin 1982). Although very limited, this evidence does support the idea of a pseudopelagic mode of life for *Seirocrinus* and other penta-crinitids.

Fecundity

The characteristically wide dispersal and low population density of pseudopelagic organisms, together with the limited availability of suitable sites for settlement of larvae, necessitates a high fecundity in such organisms. This ensures that a viable number of offspring attain reproductive maturity even though the great majority of larvae may never come close to a suitable object for settlement. Concentrations of more than 200 larval attachment discs per cm^2 have been counted on one specimen of driftwood (text-fig. 2c) from the Sinemurian of Dorset and this suggests that the larvae of *P. fossilis* may have been very abundant among the plankton at times.

The high fecundity required for a pseudopelagic mode of life, and implied by the concentration of larval attachment discs found on driftwood, may partly account for the unusually large size which pentacrinitids sometimes attained. Although a large crinoid may have a greater reproductive capacity than a smaller one, a high fecundity is often achieved in organisms by means of accelerated development and paedomorphosis. A second factor, selecting for large size, may therefore be operating in pentacrinitids.

At the present day it is found that the greatest concentration of plankton is found not at the surface of the sea but increases with depth to a maximum at about 10 m below the surface (J. W. Murray, pers. comm.). Assuming this situation to have existed in the early Jurassic it would obviously be selectively advantageous for the crinoid to feed as close to the optimum depth as is feasible. Rapid growth of the stem to a length of several metres, such as is found in *S. subangularis*, would require a highly efficient food filtration network which, as already discussed, is typical of pentacrinitids. Thus the huge size of some pentacrinitids, which has aroused so much debate in the past (Seilacher *et al.* 1968; Rasmussen 1977), serves a dual purpose and represents the optimum strategy for a pseudopelagic crinoid. It is, therefore, perhaps significant that *S. subangularis*, the largest of the Pentacrinitidae, is also morphologically the most advanced.

Attachment

An essential prerequisite for any pseudopelagic crinoid is a firm, strong attachment to the floating object. Terminal attachment discs of *P. fossilis* up to 2·5 mm across at the base have been found on one piece of driftwood (BMNH E69602), whilst a terminal disc of *Pentacrinites* sp. nov. with several attached columnals articulating by synarthries, as in larval comatulids, has been seen attached to an ammonite fragment from the Lower Sinemurian of north Somerset (BMNH E15483). Examples such as these demonstrate the method of attachment in pentacrinitid larvae but, as pointed out by Rasmussen (1977), such small attachment discs would be quite inadequate for the support of adult pentacrinitids. Since larger, adult attachment discs are never found some alternative method of attachment must have been employed. It has long been accepted that anchorage to driftwood, whether floating or sunken, is one of the primary functions of the cirri in pentacrinitids. In *Pentacrinites* the nodals in the proximal 30 cm of the stem are closely spaced and give rise to a dense mass of long flexible cirri (Pl. 36, fig. 7) which in some specimens appear to be wrapped partly around the driftwood (Pl. 36, fig. 6). Specimens showing no direct attachment to the driftwood may have used the cirri to cling onto other attached individuals.

Although the nodals are closely spaced in the proximal region intercalation of internodals distally continues indefinitely so that nodals may become very widely spaced in the distal regions of longer stems (Pl. 36, fig. 7). Cirri arising from these nodals are reduced to short vestigial remnants of more limited use for grasping objects. Similar reduction of the cirri is seen along most of the stem in *Seirocrinus* but approximation of nodals at the distal extremity of the stem has been observed by Seilacher *et al.* (1968) and Haude (1980) and provided an attachment structure in examples of this genus. In many specimens of *Pentacrinites* the distal region of the stem has been lost leaving only the cirriferous proximal region. This fact was noted by Rasmussen (1977) who considered it strong

evidence that pentacrinitids did not remain attached to floating driftwood beyond their larval stage. However, it is clear from taphonomic evidence that pentacrinitids spent most, if not all, of their life attached to floating objects despite loss of the distal parts of the stem. It is probable in the case of *Pentacrinites* that attachment was often by means of the cirri arising from a length of the stem held parallel to the log rather than by the terminal cirri alone. Furthermore, it seems improbable that attachment by the cirri was strictly passive; instead it must have involved frequent adjustments as the stem lengthened.

In the Isocrinidae, such as the contemporaneous *Chladocrinus* and *Balanocrinus*, two distinct types of columnal articulation are ordinarily present (Donovan 1984). Between adjacent internodals are developed flexible ligamentary articulations with pronounced crenulae, known as symplexies, whilst between nodals and the immediately distal internodal, or infranodal, is developed a much smoother, rigid ligamentary articulation known as a synostosis or cryptosymplexy (Donovan 1984, pl. 74, fig. 4). Synostosial articulations develop by stereom overgrowth of symplexial articulations only when internodal intercalation is complete for that particular noditaxis so that in proximal regions of the stem, where active intercalation is taking place, only symplexial articulations are found. Synostosial joints have extremely strong ligamentation but are inflexible and thought to be adapted for autotomy (Emson and Wilkie 1980). The position of synostoses beneath nodals ensures that the distal cirri are in the optimum position following autotomy. Retention of such autotomy planes in the stem would serve no useful purpose in a pseudopelagic crinoid and indeed their rigidity would decrease stem flexibility with the consequent increased risk of breakage elsewhere along the stem. It is, therefore, not surprising to find in *Pentacrinites* and *Seirocrinus* that the articulation between nodal and infranodal is symplexial (Pl. 36, fig. 8) as are all other stem joints with no evidence of synostosial articulations in any specimen examined.

The pattern of development of synostoses in the stem of isocrinids suggests a possible mechanism for their suppression in pentacrinitids. Since synostoses do not appear to develop until internodal intercalation is complete, a simple switch from definite to indefinite intercalation could result in permanent suppression of synostosial development. Indefinite intercalation of internodals is characteristic of *Pentacrinites* and *Seirocrinus* (Seilacher *et al.* 1968) and would thus appear to support this hypothesis. Furthermore, this might explain the significance of the wide nodal spacing in distal
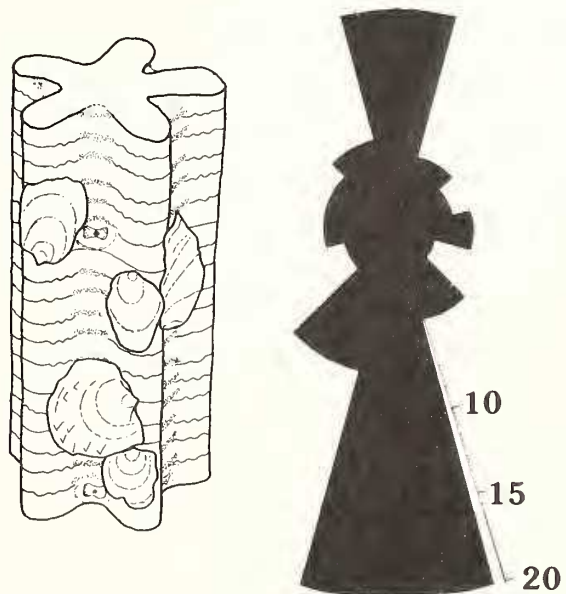
TEXT-FIG. 5. Orientation with respect to the vertical of the ventral gape in 74 specimens of the encrusting bivalve *Plicatula* sp., epizoic upon the stems of *Chladocrinus scalaris* (Goldfuss).

regions of the stem, and the consequent decrease in grasping efficiency of the cirri, a poor adaptation which cannot readily be explained in terms of functional morphology.

Epizoans as indicators of the pentacrinitid mode of life

Encrustation of living organisms by epizoans, such as certain bivalves and serpulids, has proved of some significance in the interpretation of the life orientation of fossil organisms such as ammonites (Seilacher 1960) and spiriferid brachiopods (Schumann 1967). As evidence in support of pentacrinitids having a benthic mode of life, Kauffman (1981) figured two short-stemmed specimens of *Seirocrinus* with an oyster attached to the stem, its feeding margin orientated towards the crown. He considered this to be a phototrophic response by the oyster indicating that the host crinoid lived erect in the benthic zone.

Several Lower Jurassic isocrinid species, accepted as benthic forms, are not infrequently encrusted by bivalves attached to the stem. Of 347 isolated noditaxes of *C. scalaris* (Goldfuss) from the Upper Sinemurian in my collection, 45 noditaxes were found to be encrusted by a total of 74 bivalves (*Plicatula* sp.). Measurement of the orientation of these bivalves on the stem revealed an essentially bimodal distribution (text-fig. 5) with the feeding margin in most individuals facing towards the crown or away from it, with the latter orientation favoured slightly. The intact nature of the encrusted noditaxes suggest that encrustation took place during the life of the crinoids in most cases. This evidence shows that encrusting bivalves align themselves with the stem, facing either up or down its length, and that they cannot be used to provide a way up criterion for pentacrinitids as Kauffman (1981) suggested.

Species longevity in Seirocrinus *as an indicator of the pentacrinitid mode of life*

An unusual aspect of the pentacrinitid *S. subangularis* (Miller) which has previously escaped notice is the exceptional stratigraphic range of this species. Well-preserved material from the late Carixian of Dorset (Austin and Austin 1843–1849; Lang 1936) does not show any consistent differences that distinguish it from Toarcian material from the German Posidonienschiefer. Although other Lower Jurassic crinoid species, such as *C. tuberculatus* (Miller), have a stratigraphic range of comparable duration, *S. subangularis* is apparently unique among crinoids, being the only species known to survive from the Domerian into the mid-Toarcian.

The existence of a major extinction event among marine invertebrates in the early Toarcian was first appreciated by Hallam (1961). He found that only a handful of species from the rich and diverse late Domerian faunas survived beyond the end of the *tenuicostatum* Zone at the base of the Toarcian, with much of the fauna being replaced by new species with marked mid-Jurassic affinities. Hallam (1976) records fifty-eight bivalve species from the Pliensbachian of Europe of which only sixteen are also found in the early Toarcian. Only two of these species, *Oxytoma inequivalvis* (J. Sowerby) and *Homomya gibbosa* (J. Sowerby) persist beyond the early Toarcian whilst a third species, *Meleagrinella substriata* (Lamarck) first appears in the early Toarcian and survives into the mid-Toarcian before becoming extinct. A similar pattern of extinction and replacement by new species in the early Toarcian has been documented for a number of other benthic invertebrate groups including brachiopods, foraminifera, and ostracods (Ager 1956–1967; Hallam 1961; Lord 1974).

The major faunal change seen in the early Toarcian is almost certainly a consequence of the change in facies seen in passing from the shallow-marine sands, oolites, and ironstones of the Domerian to the organic-rich shales and mudstones encountered in the Lower and Middle Toarcian. Hallam (1967) attributed this facies change to a rapid rise in sea level but to a depth insufficient to allow the development of normal marine circulation patterns, thus promoting anoxic bottom conditions. The effect of such a facies change on the benthic fauna is readily apparent but nektonic organisms might be expected to have been less profoundly affected. Of the two major nektonic invertebrate groups at this time, ammonites have proved of little use in this respect since their evolutionary rate was generally so rapid that, even under fairly constant environmental conditions, no single ammonite species would be expected to persist from the late Domerian to the mid-Toarcian. Recent work on the second of these two groups, the belemnites, has revealed that they too were profoundly affected by these facies

changes. Of the five species found in the late Domerian, four also occur in the earliest Toarcian but none persist beyond the end of the *tenuicostatum* Zone (P. Doyle, pers. comm.). Three of these species, *Passaloteuthis milleri* (Phillips), *Parapassaloteuthis zieteni* (Meyer–Eymar), and *Catateuthis longiformis* (Blake), are known only from the lower part of the *tenuicostatum* Zone whilst the fourth species, *Passaloteuthis paxillosa* (Lamarck), is not found above the top of the zone. In fact it would appear that the only fossil group which was not significantly affected by the Toarcian extinction event were the calcareous phytoplankton. Documentation of calcareous nannofossils by Hamilton (1982, pp. 28–29) has shown that of ten species present in the late Demerian, nine are also found throughout the Toarcian.

The survival of *S. subangularis* from the Carixian into the mid-Toarcian is therefore quite extraordinary considering the profound effects which the facies change at the base of the *falciferum* Zone had on organisms as diverse in habit as bivalves and belemnites. Such a stratigraphic range is matched only by calcareous phytoplankton and a very small number of other invertebrate species. It suggests that, unlike nearly all other invertebrates at this time, this species remained unaffected by changes in water depth and bottom conditions. Such an apparent immunity to these changes might be anticipated in pseudopelagic organisms which invariably are restricted to the well-oxygenated part of the water column close to the surface. Unlike belemnites, therefore, which probably made vertical migrations through the water column, pseudopelagic organisms will remain largely unaffected by changes in marine circulation patterns. This lends further support to the hypothesis that *Seirocrinus* was pseudopelagic in habit. Furthermore, of the three bivalve species which survived the Toarcian extinction event, *O. inequivalve* and *M. substriata* are both byssate forms for which a facultative pseudopelagic mode of life is not inconceivable.

DISCUSSION AND CONCLUSIONS

The evidence from the taphonomy of Lower Jurassic crinoids strongly favours a pseudopelagic mode of life for the Pentacrinitidae in contrast to the benthic habit adopted by contemporaneous isocrinids. Lower Jurassic pentacrinitids are facies independent and frequently are found fully articulated in organic-rich shales although only very rarely being represented in benthic shell beds. They are frequently found preserved beneath fairly large pieces of coalified driftwood. This evidence is consistent with a pseudopelagic mode of life, the crinoids living suspended beneath floating objects such as driftwood, and is further supported by a number of biological and morphological criteria. Rapid growth to maturity whilst the attachment site remains afloat is indicated by growth-line data and the unusual endotomous pattern of arm branching which forms an extremely efficient filtration network. A high fecundity to counteract the effects on larval success of low population density and limited availability of suitable attachment sites is indicated by the large size of adults and high concentrations of larvae settling on driftwood. Firm attachment of adults to floating objects is maintained by numerous long flexible cirri whilst autotomy planes, present at intervals in isocrinid stems, are suppressed in the pentacrinitids. Although these individual lines of evidence do not in themselves provide conclusive proof for a pseudopelagic habit, their consistent support for this mode of life when considered together casts very considerable doubt on any interpretation of a strictly benthic mode of life for Lower Jurassic pentacrinitids.

Buckland (1836) originally suggested a pseudopelagic habit for pentacrinitids on the basis of observations that *Pentacrinites fossilis* occurs beneath lenticles of coalified driftwood on the Dorset coast. Seilacher *et al.* (1968) obtained further evidence in support of this hypothesis from examination of a large group of *S. subangularis* from the Posidonienschiefer, now preserved in the Geological Institute of Tübingen University. The arms of these crinoids are spread radially and lie beneath the stems suggesting that the crowns reached the sea-floor first. Similar preservation has also been seen in *P. fossilis* from Dorset (BMNH E69840). The bundled stems in the Tübingen specimen were also noted and are a common feature of many Dorset specimens (Pl. 36, fig. 7; also BMNH E69840 and E25102). Tangling of the stems in this manner was perhaps the result of vortices caused by the driftwood as it sank through the water column. More recently Seilacher (1982) has noted that

specimens of *Seirocrinus* from the Posidonienschiefer point upcurrent as might be expected for crinoids dragging behind a sinking piece of driftwood but contrary to the orientation which crinoids attached to a benthic island might assume.

However, the major theme of the earlier paper (Seilacher *et al.* 1968) concerns the functional morphology of the stem in *Seirocrinus*. They found that flexibility was apparently greatest towards the distal end of the stem and decreased proximally. This contrasted with the pattern observed in the Middle Triassic *Encrinus*, a benthic crinoid in which stem flexibility increases proximally, but conforms to the paradigm for stem flexibility in a pseudopelagic crinoid. These interpretations of stem flexibility are, however, based upon the size, shape, and spacing of skeletal elements whereas it has been suggested that collagen ligaments are the primary control on rigidity (Meyer 1971*b*; Kauffman 1981). Since no extant crinoids possess a stem resembling that of pentacrinitids the actual flexibility of the fossil stems cannot be determined although interpretations based upon stem morphology (Seilacher *et al.* 1968; Haude 1980) probably represent a reasonable approximation.

Alternatives to a pseudopelagic mode of life for pentacrinitids have been suggested by a number of authors. Loriol (1878) suggested that adult *Pentacrinites* with a short column and numerous cirri could swim by means of the latter and also attach to foreign objects. Kirk (1911) also considered the long greatly compressed cirri of *P. fossilis*, *P. dargniesi* (Terquem and Jourdy), and *P. dichotomus* [= *P. collenoti* (Loriol)] to be well adapted for swimming. The hypothesis of a combined swimming and attachment function for the flattened and hooked cirri of *P. dichotomus* (M‘Coy) [= *P. quenstedti* (Oppel)] has recently been revived (Hauff 1984). However, the cirri of crinoids are not capable of the strong rapid movements necessary for swimming since they entirely lack striated muscle fibres (Holland and Grimmer 1981). The possibility that adults lived freely floating has also been considered (Loriol 1877–1879) but there is no firm evidence in support of this.

The most frequently considered alternative to a pseudopelagic habit in pentacrinitids is that of a benthic mode of life. Abel (1927) considered that crinoid larvae settled on sunken driftwood which was subsequently brought into the South German Sea at Holzmaden by turbulent currents caused by a storm. This seems improbable considering the delicate nature and intact preservation of these crinoids. Rasmussen (1977, 1978) discussed several lines of evidence in support of a benthic mode of life for the Pentacrinitidae. In the introduction to his earlier (1977) paper he described the stems of both Isocrinidae and Pentacrinitidae as possessing cryptosymplexial articulations below the nodal columnals. This is certainly true of the Isocrinidae but, as discussed earlier, this type of articulation is entirely lacking in pentacrinitid stems and, in my view, this is an important adaptation for a pseudopelagic mode of life. Rasmussen’s main lines of argument against a pseudopelagic habit concerned the mode of attachment and the growth rate of these crinoids. He found it ‘inconceivable that larval crinoids, attaching to floating trunks, would remain attached by the terminal disc and the thin and fragile column during many years, growing up to adult specimens and reaching the considerable size of 30–40 cm in length of arms, before the trunk stranded or sank to the bottom waterlogged and overgrown by *Pseudomytiloides*’ (Rasmussen 1977, p. 55). These objections have been discussed earlier and shown to be largely unfounded.

The benthic mode of life which Rasmussen favoured for pentacrinitids neither explains in any way the frequent presence of pentacrinitids in organic-rich deposits lacking any other benthic organisms nor accounts for the consistent occurrence of coalified driftwood lying above the crinoids rather than beneath them. However, he provided an alternative interpretation for the preservation of pentacrinitids with the oral surface of the crown facing downwards and the arms spread radially, as described by Seilacher *et al.* (1968). He considered that in specimens with a long column the proximal region may droop under the weight of the crown as the crinoid dies and so the crown would touch the bottom with its oral side downwards. Haude (1980) subsequently contested this hypothesis on the grounds that it contradicts the constructional morphology described by Seilacher *et al.* (1968) for the stem of *Seirocrinus*.

Kauffman (1981), in a major reinterpretation of the ecology of the Toarcian Posidonienschiefer, devoted considerable attention to the mode of life of the crinoids found therein. He challenged the pseudopelagic crinoid hypothesis using several lines of evidence, much of it based upon Rasmussen’s

(1977, 1978) work, but also failed to appreciate the fundamental differences in morphology which distinguish isocrinids and pentacrinitids. Although he states that no pseudopelagic crinoids are known today this cannot be used as evidence that they did not exist in the past since the Pentacrinitidae became extinct in the late Jurassic. In common with most previous proponents for a benthic mode of life in pentacrinitids, Kauffman regards the Posidonienschiefer *Seirocrinus* as too large and old to have been attached to floating driftwood all of their lives yet he provides no evidence in support of this claim. His additional statement, that driftwood rarely remains afloat for more than a year, seems an unduly low estimate in the light of more recent evidence, whilst the abundance of larval crinoid attachment discs on some pieces of driftwood would appear to contradict his claim that driftwood is a poor substrate for settlement of epizoans. The use of organisms epizoic upon crinoid stems for determining the mode of life of pentacrinitids has been discussed earlier and shown to be inconclusive.

Kauffman concluded that the crinoids lived as benthos attached directly to the substratum or to sunken driftwood by the cirri. He suggested that death was due to an overturn of anoxic bottom waters and that the dying crinoids came to rest in a thin benthic, anoxic zone at or slightly above the sediment-water interface where they were protected from scavenging and decay. This is perhaps the case for the intact isocrinids (WARMS G9921; OUM J3231) encountered extremely rarely in Hettangian finely laminated shales on the Dorset coast. However, if such a benthic mode of life was true of pentacrinitids it seems remarkable that contemporary isocrinids, unquestionably regarded as benthos, are entirely excluded from the organic-rich deposits in which pentacrinitids are most frequently encountered.

My own conclusion from the taphonomic, morphological, and palaeobiological evidence is that Lower Jurassic pentacrinitids adopted a pseudopelagic mode of life attached to floating objects, particularly driftwood. Although being essentially obligate pseudoplankton, evidence from certain specimens suggests that they could survive for a time as benthic crinoids if they sank into a suitable environment. However, there is no conclusive evidence to support previous claims for a strictly benthic mode of life for these crinoids.

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